

Interplay of seasonal sunlight, air and leaf temperature in two alpine páramo species, Colombian Andes

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ABSTRACT

In models of photosynthetic gas exchange, leaf temperature (T_{leaf}) is often calculated using a combination of derivations of the energy balance equation and measurements of air temperature (T_{air}). Yet, there are frequently large differences between T_{leaf} and T_{air} under natural field conditions, and an energy balance is complicated in complex canopies, especially in tropical ecosystems. In the present study, we aimed to quantify the variation in T_{leaf} relative to T_{air} under naturally varying PPFD values in two representative species (*Espeletia grandiflora* and *Chusquea tessellata*) of a tropical alpine ecosystem (páramo, Colombian Andes) during both wet and dry seasons. The results of a Structural Equation Model showed that T_{leaf} was strongly correlated with changes in T_{air} during both seasons, but large differences (up to 14 °C) occurred between T_{air} and T_{leaf} during the dry season when PPFD varied the most, especially in *C. tessellata*. Thus, using T_{air} to approximate T_{leaf} under variable conditions of incident sunlight could generate substantial errors in estimates of temperature-sensitive physiological processes. These results should be valuable for evaluating the accuracy of carbon and water exchange models within current and future scenarios of climate change in tropical páramos, as well as other ecosystems.

1. Introduction

Accurately calculating ecosystem gas exchange and thus, gross and net primary productivity, is fundamental in our understanding and our predictions of how climatic changes may affect ecosystems. Understanding how leaf temperature (T_{leaf}) varies is crucial in this regard, because respiration and photosynthesis are strongly dependent upon T_{leaf} (e.g. Berry and Björkman, 1980). Models often evaluate the effects of increasing air temperature, as a proxy to T_{leaf} , on ecosystem processes (Cramer et al., 1999; Rowland et al., 2015). However, using T_{air} instead of T_{leaf} to characterize the environment of vegetated ecosystems can lead to inaccurate estimates of carbon and water dynamics (De Frenne and Verheyen, 2016), especially for species or habitats where significant differences between leaf and air temperatures occur. Changes in leaf temperatures are the result of changes in net solar and thermal radiation, conductive and convective heat exchange, and latent heat loss (assuming negligible effects of heat storage and metabolic heat

production) at a given moment (Campbell and Norman, 1998). Several models have therefore used an energy balance approach on numerous levels within the plant canopy to estimate leaf temperature (Dai et al., 2004; Leuning et al., 1995; Metzger et al., 2015). This approach is common in large-scale models of gas exchange in forests (e.g., CLM 3.5, ED2, JULES, SiB3 and SPA; Rowland et al., 2015) and in peatlands (e.g., InTec, McGill, ECOSSE; Ju and Chen, 2005; St-Hilaire et al., 2010; Bell et al., 2012). However, the energy balance experienced by individual leaves also involves a host of biotic factors such as leaf angle and orientation, plant spacing and architecture (Kitajima et al., 2005), which complicates a simplified solution to the energy balance equation. Given the complexity of parameterizing an energy balance model, an alternative is the use of empirical correlation models. These models have been used successfully for estimating soil temperatures from air temperature measurements under forest cover (Bond-Lamberty et al., 2005), to predict stomatal conductance in response to changes in temperature and sunlight incidence (Collatz et al., 1991; Leuning

Abbreviations: GSR, global solar radiation (W m^{-2}); RH, relative humidity (%); SEM, structural equation model; SVP, saturated vapor pressure (kPa); PPFD, photosynthetic photon flux density ($\mu\text{mol m}^{-2} \text{s}^{-1}$); PPFD_L, photosynthetic photon flux density incident on a leaf ($\mu\text{mol m}^{-2} \text{s}^{-1}$); PPFD_{site}, photosynthetic photon flux density incident on a horizontal plane ($\mu\text{mol m}^{-2} \text{s}^{-1}$); pPPFD, theoretically predicted values of potential photosynthetic photon flux density ($\mu\text{mol m}^{-2} \text{s}^{-1}$); T_{air} , air temperature (°C); TOD, time of day; T_{leaf} , leaf temperature (°C); VPA, vapor pressure of ambient air (kPa); VPD, vapor pressure deficit (kPa)

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et al., 1995), or to quantify T_{leaf} variability in a semi-deciduous lowland tropical forest (Rey-Sánchez et al., 2016).

Tropical alpine ecosystems, occurring in the mountain ranges of the Northern Andes, the afroalpine belt, and the islands of Borneo and Papua New Guinea between the altitudes of ca. 3000–3500 m to 5000 m (Smith, 1994), are characterized by extreme environmental conditions. The Northern Andes has the largest area of the alpine ecosystem known as the páramo (Buytaert et al., 2011), with the largest area found in Colombia. The high weather variability of the páramo (as it occurs in other tropical alpine ecosystems) is reflected in low atmospheric pressure, large daily temperature fluctuation (high daytime and low nighttime temperatures), intense ultraviolet radiation, high and variable solar radiation, and high wind speed (Luteyn, 1999; Körner, 2003). Even though the páramo has high plant diversity (3431 species of vascular plants described), of which a majority are endemic (> 60%, Luteyn, 1999), it has not received as much attention as other species-rich ecosystems such as the lowland forests of the Neotropics (Hoorn et al., 2010). Páramos are important for the large variety of ecosystem services they provide, including biodiversity, large soil carbon storage in the form of peat, and the regulation of water supply for municipalities, agriculture, and hydroelectric power (Buytaert et al., 2011). For example, most of the human population in Colombia depends on water supply from this ecosystem (Ruiz et al., 2008; Buytaert et al., 2011). However, these ecosystem services, related to hydrological and physiological processes in plants, may be severely impacted in the coming decades as global temperatures continue to rise and threaten the distribution and species composition of the páramo (Buytaert et al., 2011).

Montane forests are not explicitly taken into account in global climatic models (e.g., DGVMs or dynamic global vegetation models) and few studies have recently approached these ecosystems using case-studies (e.g., Fischer et al., 2015; Fyllas et al., 2017; Paulick et al., 2017). Although in many areas of the world, montane ecosystems, and in particular alpine ecosystems such as the páramo, play a key role in water provisioning, they are yet to be included in global models. Therefore, in the present study we aim to provide baseline data on the interplay of T_{leaf} and other microclimate variables. Our first objective was to build a record of microclimate data for both wet and dry seasons of one of the most important páramos in Colombia, the Chingaza National Park. Our second objective was to calculate the interplay of incident sunlight (photosynthetic photon flux density, $PPFD$), on measured differences in T_{air} and T_{leaf} for two common páramo species of the northern Andes. To this end, we used a Structural Equation Model (SEM) to quantify the effects of $PPFD$, T_{air} and relative humidity (RH) on T_{leaf} during the wet and the dry season. We also present comparisons between measured $PPFD$ and theoretically predicted values ($pPPFD$) based on known effects of latitude and altitude. Given that incoming radiation is extremely variable in the páramo (Körner, 2003; Dye et al., 2009; Sanchez et al., 2014) and that it is a major variable in energy balance equations, as well as the empirical model developed for a semi-deciduous tropical forest in Panamá (Rey-Sánchez et al., 2016), we decided to study this variable in more detail to show the diurnal and season variability of incoming solar radiation and its influence on T_{air} and T_{leaf} .

2. Materials and methods

To test the efficacy of using T_{air} as a proxy for T_{leaf} , our general approach was to measure differences in the two under the highly variable sunlight regime of a Colombian páramo during both wet and dry seasons. Measured sunlight levels were recorded at a central location at the research site as well as from $PPFD$ sensors on individual leaves of selected plants.

2.1. Study site and species

The study site was located in Chingaza National Park (Chingaza; Eastern Cordillera, Colombia), ca. 66 km away from the capital of Colombia (Bogotá). This park comprises a protected area of more than 50,000 ha between 4°20′–4°50′ N and 73°30′–73°55′ W, and an altitudinal range that varies between 800–4000 m. Above ~3200 m, the vegetation changes from high-elevation mountain forests to the alpine páramos where more than 350 plant species occur. Chingaza has been classified as a humid páramo (Cleef, 1981; Sarmiento, 1986) and is considered as one of the most important páramos because it provides ca. 80% of the municipal drinking water to the capital of Bogotá, Colombia (Vásquez and Serrano, 2009).

Chingaza has a seasonally unimodal precipitation regime with a wet season typically lasting from April through November and a short dry season from December to late February or early March (Sarmiento, 1986). At 3500–3600 m (close to the site of Laguna Seca), mean monthly T_{air} varies between ~6 and 10.5 °C with maximums greater than 20 °C and nighttime minimums several degrees below freezing (Cardenas et al., 2002). Temperatures are more variable during the dry season, reaching minimum values below 0 °C, whereas during the wet season nighttime temperatures rarely go below freezing (Tol and Cleef, 1994; Cardenas et al., 2002). The annual precipitation maximum and minimum are highly variable, ranging between 1690 and 3320 mm, with an annual mean of ca. 2000 mm (Tol and Cleef, 1994; Cardenas et al., 2002). Based on a 20-year wind record (1980–2000) for the area near Chingaza, wind speed is significantly lower during the dry (1.9 m/s) versus wet season (2.7 m s⁻¹) (t -test, $P < 0.001$). See http://www.upme.gov.co/Atlas_Viento.htm.

Within Chingaza, we did our sampling near the site of Laguna Seca (4°41′00.2″ N, 73°47′14.5″ W and 3655 m elevation). We considered these sites representative of the páramo of this region based on elevation, topography, species composition, and climate (Parque Nacional Natural Chingaza, 2005–2009). The two species chosen for study (Fig. 1) were *Espeletia grandiflora* Bonpl. (Asteraceae) and *Chusquea tessellata* Munro (Poaceae), both dominant sympatric members of the Chingaza páramo community. For a more detailed description of this habitat and species composition see Sanchez et al. (2014).

2.2. Environmental measurements

A meteorological station was deployed in an open area located a few meters away (ca. 3–8 m) from the natural vegetated area where plants were monitored. The measurements were taken between December of 2012 and May of 2014 and covered two dry seasons (December–February) and one wet season (March–November). All sensors were placed at 1.5 m above the ground. We quantified air temperature (T_{air}) and relative humidity (RH) using five DS1921G Thermochron® (accuracy: ± 1 °C) and two DS1923 Hygrochron® ibutons® (accuracy: ca. 0.04% RH and ± 0.5 °C). These measurements were recorded in 1-min intervals during the 18-month period. Photosynthetic photon flux density ($PPFD_{site}$ in $\mu\text{mol m}^{-2} \text{s}^{-1}$, 400–700 nm) was measured in 5 s intervals using a Quantum sensor (Li-Cor, LI-190) attached to a Process 101A MidgeTech datalogger for a 14-month period (December 2012 through May 2013 and October 2013 through May 2014). Global solar radiation (GSR in W m^{-2} of 400–1100 nm wavelengths) was recorded in 5-s intervals using a Pyranometer (LI-200) attached to a Process 101A MidgeTech datalogger for an 11-month period (December 2012 through May 2013 and November 2013 through March 2014). Since precipitation is highly variable, we decided to build a longer record using a digital pluviometer (RI-Loader 2.2) for recording precipitation from January 2013 to May 2014 in addition of the historical precipitation data, from 1987 to 2012, obtained from the meteorological station of the Empresa de Acueducto y Alcantarillado de Bogotá (EEAB) at Laguna Seca. Vapor pressure deficit (VPD) of the air was calculated as saturated vapor



Fig. 1. Study species, *Espeletia grandiflora* (rosette) and *Chusquea tessellata* (bamboo) at the field site (left). Detail of *Chusquea* (upper right) and *Espeletia* leaves (bottom right) including sensors recording photosynthetic photon flux density ($PPFD_i$) incident on adaxial leaf surfaces.

pressure (SVP) minus actual vapor pressure of the ambient air (VPA). Actual vapor pressure was calculated as $(\%RH \times SVP)/100$ (Murray, 1967).

2.3. Leaf temperature and incident sunlight

Leaf temperature (T_{leaf}) and $PPFD$ incident on the adaxial surface of leaves ($PPFD_i$) was measured for five days every month, during a 10-month period (December 2012 through May 2013, and November 2013 through February 2014; these measurements were not recorded between June and October of 2013). Four healthy, mature, fully expanded, south-facing leaves corresponding to four different individuals were selected for each species per month and each month we chose different individuals per species. We measured a total of 40 leaves per species during the 10-month interval. T_{leaf} was recorded using light-weight fine-wire (36 ASU gauge), copper-constantan thermocouples while $PPFD_i$ was measured using GaAsP light sensors (G1118 Hamamatsu; Fig. 1). The thermocouples were placed in the lower half of the underside of the leaf; they were wrapped around stems and petioles without affecting leaf angle, and only made contact with a fixed area through the five days of each field campaign. The $PPFD_i$ sensors, as well as the thermocouples, were connected to a Campbell multiplexer (AM16/23B and AMT25, respectively; Campbell Scientific, Utah) and data recorded by a Campbell datalogger (model CR-1000, Campbell Scientific, Utah). All T_{leaf} sensors were logged every minute and the $PPFD_i$ sensors every 10 s.

2.4. Potential $PPFD$ ($pPPFD$)

Incoming radiation has been found to increase by 8% with every

1000 m of elevation (Blumthaler et al., 1997). In addition, in mountainous sites radiation reflection from clouds often increases the amount of incident sunlight. To evaluate these effects, we calculated potential $PPFD$ ($pPPFD$), defined as $PPFD$ incident on a horizontal plane assuming cloudless conditions at the research site. To obtain instantaneous $pPPFD$, we first calculated sun zenith angle (the angle measured from the vertical) every five seconds using a mathematical coordinate representation of the Sun-Earth orbit geometry (Campbell and Norman, 1998). We then calculated direct and diffuse sky $PPFD$ assuming a constant atmospheric transmittance of 0.75 (Gates, 1980, Pearcy et al., 1989) and a constant $PPFD$ at the outer edge of the atmosphere equal to $2790 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Pearcy et al., 1989); the elevation was 3655 m. The equations used to estimate $pPPFD$ assume that sunrise and sunset occur when the sun disk is at the horizon (i.e., day length assuming a 180° sky hemisphere), while in fact twilight can occur when the sun is 6° below the horizon (Campbell and Norman, 1998). As a result, $pPPFD$ was lower than $PPFD_{site}$ at the beginning and end of the day (data not shown). We empirically adjusted for this difference by calculating $pPPFD$ for a 182° day length. This adjustment resulted in a very close match between $PPFD_{site}$ and $pPPFD$ for most of the day. However, to minimize potential discrepancies inherent to the model, we only used values between 0700 and 1800 h.

2.5. Data analysis

Herein, daytime and nighttime measurements were considered separately, except for the analysis of air and leaf temperature differences (ΔT). Sunrise, solar noon and sunset times were calculated with Sun-Earth orbit geometry equations for the latitude of the site (Campbell and Norman, 1998). Nighttime for Julian day (j) corresponded to the

time from sunset to midnight of day j plus the time from midnight to sunrise of day $j + 1$. $PPFD_{site}$ and $PPFD_l$ events were averaged at 1 min intervals in order to compare them with recorded temperatures. We calculated daily means and used t-tests and analyses of variance (ANOVA) to compare all of the environmental measurements ($PPFD_{site}$, T_{air} , VPD, precipitation, T_{leaf} and $PPFD_l$) for the wet and the dry seasons. We also calculated the averages per hour for each of the environmental variables, as well as for the difference between T_{leaf} and T_{air} ($\Delta T = T_{leaf} - T_{air}$) for each species per season. To evaluate the relationship between variables such as GSR and $PPFD_{site}$, T_{air} and $PPFD_{site}$, T_{air} and T_{leaf} , $PPFD_{site}$ and T_{leaf} , and $PPFD_l$ and T_{leaf} , we used least square regression analyses. Several models were tested (e.g., linear, logarithmic, exponential, polynomial of 2–4 factors) and the relative goodness fit of the models was assessed using the Akaike Information Criterion (AIC). Analyses of covariance were also used to assess the significance of the three models with highest AIC score. All the above analyses employed R version 3.2.0 (R development core team 2015).

A Structural Equation Model (SEM) was used to create an empirical model for predicting the response of T_{leaf} to environmental variables. The SEM was created employing a software developed by SPSS named AMOS (Arbuckle, 2006). We created different models including several paths between different environmental drivers, including: $PPFD_{site}$, $PPFD_l$, T_{air} , RH, VPD and time of day (TOD). TOD is a variable spanning from approximately, 0600 to 1800 h and with a non-linear relationship with the other variables. To guarantee linearity between all relationships, TOD was transformed using a second-order polynomial function. All the other variables were transformed to their natural logarithm to improve linearity. For the SEM, we used measurements taken every 10 min and calculated 10 min means for the leaf data. In each case, the model with the best-fit was selected using maximum likelihood chi-square and the corresponding AIC score.

3. Results

3.1. Environmental measurements

Although the precipitation record at Laguna Seca spanned from 1987 to 2014, there was a complete record for only 11 years (non-missing data). For those years, total mean annual precipitation was 2171 mm, with 2960 mm for the wettest year on record (2011) and 1843 mm for the driest year (1994). During 2013 average rainfall was 2133 mm. The driest month was January, with an average of 56 mm. July was the wettest month (average of 292 mm) on record, but April of 2011 was the rainiest (585 mm). Mean monthly precipitation was significantly different between the dry (70 mm) and the wet season (209 mm; $P < 0.001$).

The dry season (December–February) had significantly higher mean daytime T_{air} , global solar radiation (GSR; data not shown) and incident sunlight ($PPFD_{site}$) than the wet season (March–November; t-test, $P < 0.001$; Fig. 2). T_{air} commonly fell below 0 °C between 1800 and 0600 h during the dry season, while this occurred in very few occasions in the wet season (Fig. 2). However, the highest T_{air} (25 °C) was nearly the same for both seasons. $PPFD_{site}$ was higher during the mornings of the dry season, compared to the afternoons, creating a skewed distribution (Fig. 2; see below Section 3.3). VPD was substantially lower during the wet season (0.052 kPa) compared to the dry season (0.16 kPa; $P < 0.001$), and the maximum VPD was registered during the dry season between noon and 1300 h (0.55 kPa; data not shown). The model that best described the relationship between GSR and $PPFD_{site}$ was a linear model ($P < 0.001$; $r^2 = 0.99$) with a slope of 1.98 (data not shown). Because there was a strong relationship between GSR and $PPFD_{site}$, and we have a more complete data set for $PPFD_{site}$, we used $PPFD_{site}$ as a proxy for GSR when referring to the possible heating effect of PPFD on T_{leaf} .

3.2. Leaf temperature (T_{leaf})

Overall, mean T_{leaf} was significantly higher during the dry season for both species ($P < 0.001$), although *E. grandiflora* had a significantly higher daily mean T_{leaf} than *C. tessellata* in the dry and wet season (7.3 vs. 7.1 °C, $P < 0.01$ and 6.8 vs. 6.7 °C, $P < 0.01$, respectively) (Fig. 3). Highest T_{leaf} for both species was over 30 °C around noon during both seasons. Minimum dry season T_{leaf} was -2.5 and -2.2 °C for *E. grandiflora* and *C. tessellata*, respectively, and below freezing T_{leaf} was common between 1900 h and 0600 h (Fig. 3). During the wet season, minimum T_{leaf} was close to 0 °C in both species. Absolute variation of T_{leaf} was higher during the dry season, with maximum temperature changes of over 35 °C; average difference between highest and lowest T_{leaf} in the dry season was more than 10 °C, compared to ca. 5 °C in the wet season.

A significant linear relationship occurred between T_{leaf} and T_{air} for both seasons ($r^2 > 0.98$; one-way ANOVA, $P < 0.001$; data not shown). The slopes for both seasons were equal to or slightly higher than 1 (*C. tessellata* dry = 1, wet = 1.03; *E. grandiflora* dry = 1.05, wet = 1.04; ANCOVA, $P > 0.05$). During the wet season, both species had slightly higher T_{leaf} than T_{air} during daytime hours and this pattern was especially clear in *E. grandiflora* (Fig. 4). During the dry season, there was more variation in ΔT , especially in *C. tessellata*, where ΔT varied ± 4 °C at 1200 h (Fig. 4). Between 0900 and 1700 h, *C. tessellata* had median ΔT values below 0 °C (cooler than T_{air}), while in *E. grandiflora* ΔT values were higher than 0 °C (warmer than T_{air}). During daytime hours, T_{leaf} was significantly different from T_{air} in both species and both seasons ($P < 0.001$).

Nighttime T_{leaf} varied little in the wet season and ΔT remained near 0 °C, with an average variation of less than 1 °C (Fig. 4). During the dry season ΔT at night had a variation of ca. 3 °C (in *C. tessellata* at 300–500 h and 1900–2100 h). However, leaves of both species were, in general, slightly warmer than nighttime T_{air} and T_{leaf} remained significantly different from T_{air} in both species and both seasons ($P < 0.001$).

3.3. PPFD, T_{air} , and T_{leaf}

The relationship between T_{air} (measured every min) and $PPFD_{site}$ was asymptotic in both seasons (polynomial model of 4 factors; $P < 0.001$; $r^2_{dry} = 0.6$, $r^2_{wet} = 0.51$). At low $PPFD_{site}$ there was a rapid increase in T_{air} and the relationship changed rapidly (beginning at 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$) with increasing $PPFD_{site}$ (Fig. A1).

The relationships between T_{leaf} and both $PPFD_{site}$ and $PPFD_l$ were also asymptotic for both species and both seasons ($P < 0.001$), although there were clear differences between the dry and the wet season (Fig. A2; $PPFD_l$ not shown). During the dry season, lower T_{leaf} was associated with PPFD close to zero (early morning or evening). In *C. tessellata*, highest T_{leaf} (~ 25 °C) did not correspond with highest PPFD values, while highest T_{leaf} (~ 28 °C) corresponded with some of the highest PPFD values (2000–2500 $\mu\text{mol m}^{-2} \text{s}^{-1}$) in *E. grandiflora*. In contrast to T_{air} , the response of T_{leaf} to $PPFD_{site}$ increased linearly after $\sim 400 \mu\text{mol m}^{-2} \text{s}^{-1}$ in both species (Fig. A2; $P < 0.001$). However, during the wet season, warmest T_{leaf} corresponded with the highest PPFD values (~ 2000 – $2300 \mu\text{mol m}^{-2} \text{s}^{-1}$) in both species.

Based on the equations used to derive potential PPFD ($pPPFD$), the highest potential light values ($\sim 2465 \mu\text{mol m}^{-1} \text{s}^{-2}$) occurred at the solar equinoxes in March and September. Given that our field site is slightly north of the equator, December was expected to have the overall lowest $pPPFD$, and modeled values resulted in maximum values close to 2175 $\mu\text{mol m}^{-1} \text{s}^{-2}$ (Fig. A3). Events over $pPPFD$ were not uncommon, especially at high light intensities ($> 2000 \mu\text{mol m}^{-1} \text{s}^{-2}$; Fig. A3). During the wet season, these events lasted more than 30 min, while during the dry season, the maximum duration was 25 min (results not shown). However, for both seasons the most common duration for events above $pPPFD$ was between 1 and 2 min. Values over

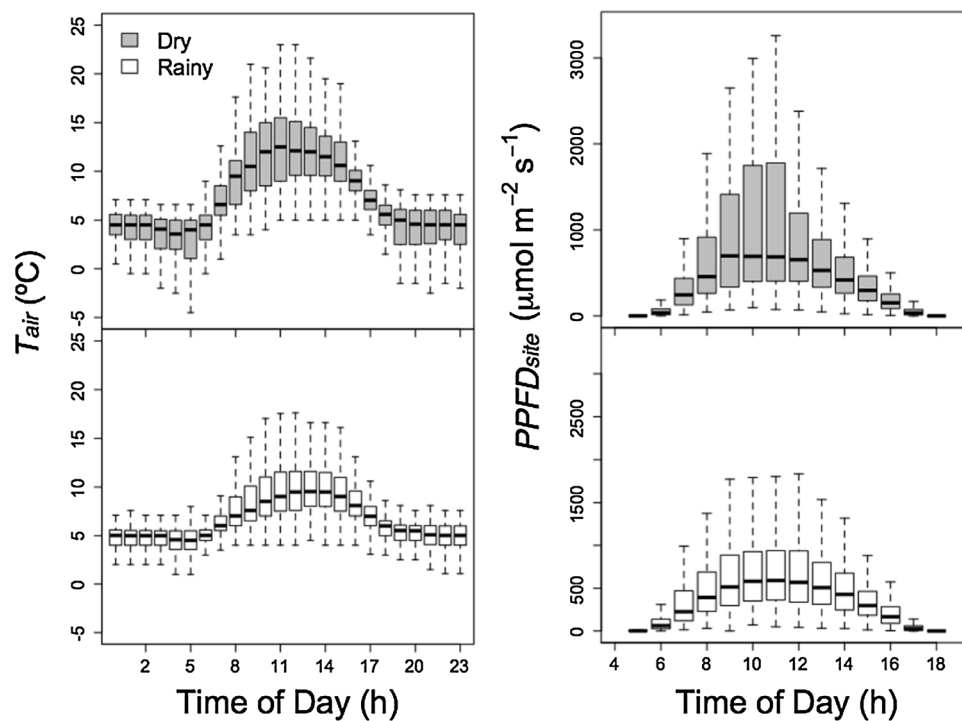


Fig. 2. Air temperature (T_{air}) and photosynthetic photon flux density measured at the site ($PPFD_{site}$) for the dry (grey) and the rainy season (white). Boxplots indicate the median, 25th and 75th percentile. Whiskers extend to 1.5 times the interquartile range. There were significant differences between seasons ($P < 0.001$).

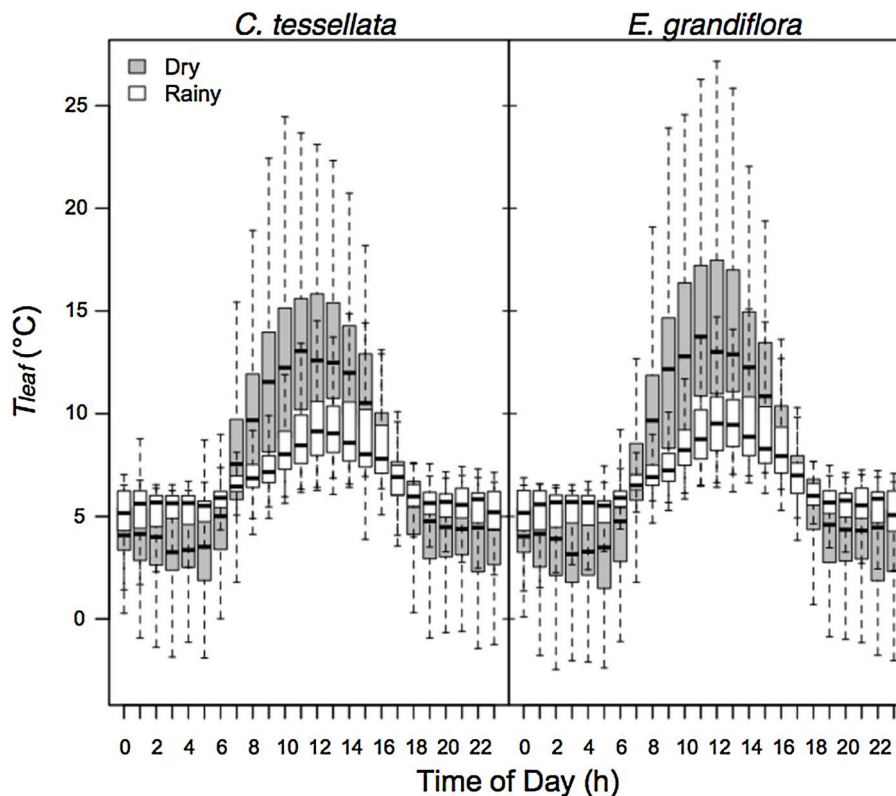


Fig. 3. Boxplots of leaf temperature (T_{leaf}) variation during the dry (grey) and the rainy season (white) for *C. tessellata* and *E. grandiflora*. Boxplots indicate the median, 25th and 75th percentile. Whiskers extend to 1.5 times the interquartile range. There were significant differences between the dry and wet seasons in both species ($P < 0.001$).

$3000 \mu\text{mol m}^{-1} \text{s}^{-2}$ occurred in most months recorded (with the exception of April) and were not uncommon during the wet season. These extreme $PPFD$ events lasted as long as 4 min during the wet season (in October), while they never occurred for more than 1 min at a time during the dry season. The absolute highest $PPFD_{site}$ value was

$3646.4 \mu\text{mol m}^{-1} \text{s}^{-2}$, recorded in October of 2013 (a wet season month, Fig. A3) and the highest value during the dry season was $3396 \mu\text{mol m}^{-1} \text{s}^{-2}$ in February of 2014. However, it is important to recognize that, although maximum $PPFD$ values over $2500 \mu\text{mol m}^{-1} \text{s}^{-2}$ were not uncommon, all days in both seasons had a

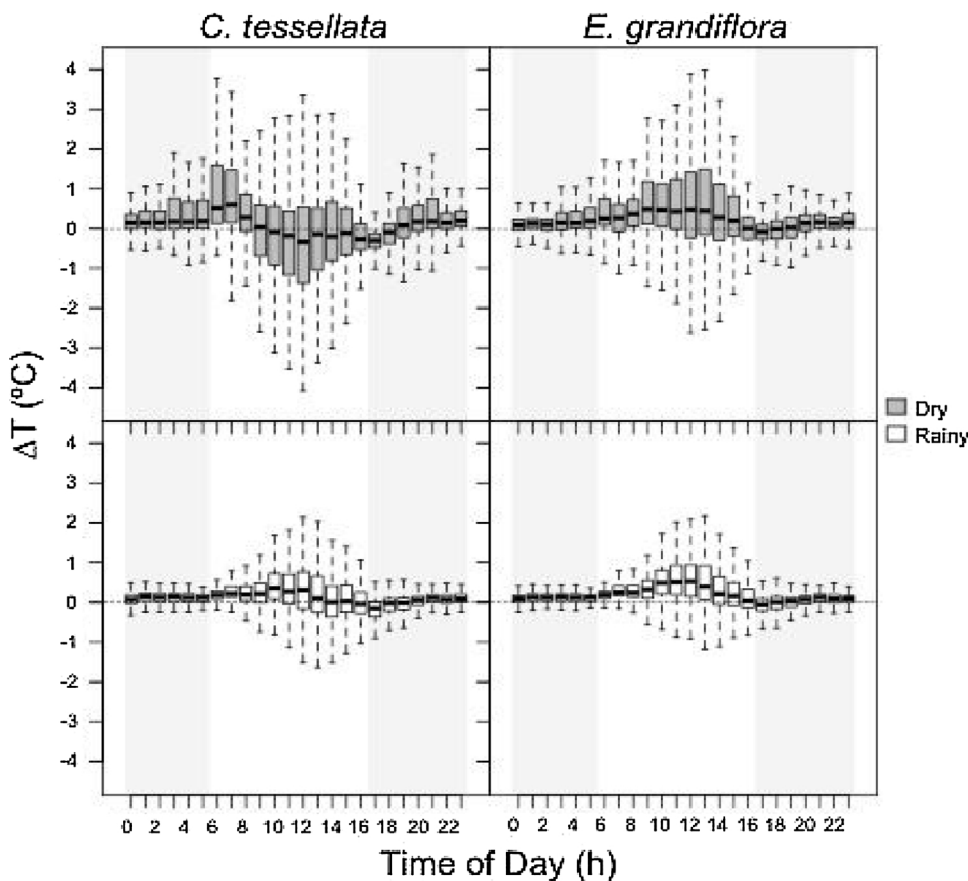


Fig. 4. Boxplots of ΔT ($T_{leaf} - T_{air}$) variation during the dry (grey) and wet season (white) for *C. tessellata* and *E. grandiflora*. The grey-shaded areas are night-time temperature differences. Boxplots indicate the median, 25th and 75th percentile. Whiskers extend to 1.5 times the interquartile range. There were significant differences between the dry and rainy seasons in both species ($P < 0.001$).

lower daily average $PPFD$ than the daily average $pPPFD$ (e.g., Fig. A3).

3.4. $PPFD_{site}$ versus ΔT ($T_{leaf} - T_{air}$)

During the dry season, ΔT covered a wide range of $PPFD_{site}$ values

(Fig. 5) while substantially less variation occurred during the wet season. The relationship between ΔT and $PPFD_{site}$ was linear above a $PPFD_{site}$ of $100 \mu\text{mol m}^{-2} \text{s}^{-2}$ for both species during the wet season ($y = 0.001x - 0.1115$; $r^2 = 0.2$, $P < 0.001$ in *C. tessellata* and $y = 0.001x - 0.0265$; $r^2 = 0.32$, $P < 0.001$ in *E. grandiflora*), but the

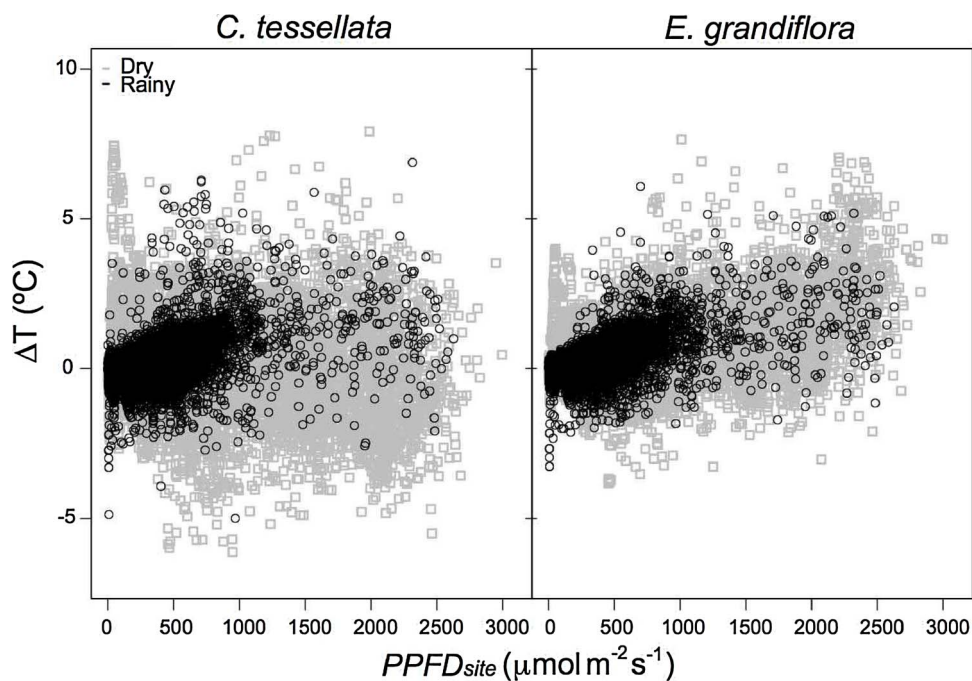


Fig. 5. Relationship between incident sunlight measured at the site ($PPFD_{site}$) and the difference between leaf and air temperature measured at the site ($\Delta T = T_{leaf} - T_{air}$) for *C. tessellata* and *E. grandiflora* during both the wet and dry seasons.

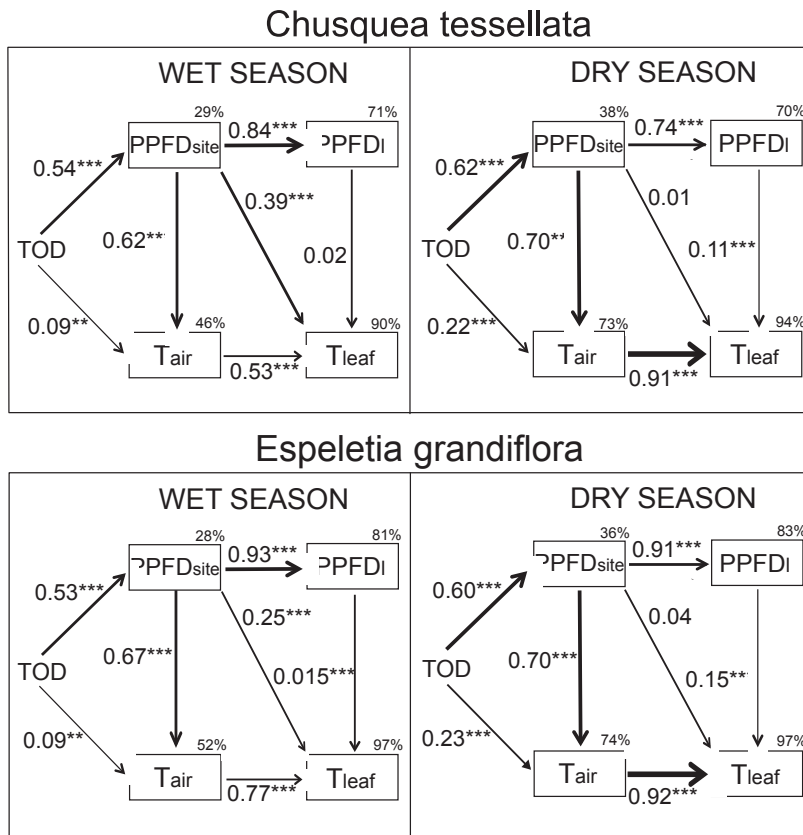


Fig. 6. Path analysis showing the interactive effects of environmental variables on leaf temperature (T_{leaf}) during the wet and dry season in *C. tessellata* and *E. grandiflora*. Each arrow represents a causal relationship between two variables. Variables in boxes are endogenous variables (dependent on other variables) and variables without boxes are exogenous (independent). The strength of the relationship is represented by the width of the arrow and by the contiguous path coefficient (β) with its level of statistical significance (** $P < 0.005$, *** $P < 0.001$). β indicates the strength of the relationship and varies between 0 and 1. The percentage of the variance that is explained by each variable is shown above each box on the right-hand side. Abbreviations: time of day (TOD), photosynthetic photon flux density incident on the leaves (PPFD_l), photosynthetic photon flux density measured at the site (PPFD_{site}), air temperature (T_{air}), leaf temperature (T_{leaf}).

slope was closer to zero for *C. tessellata* during the dry season ($y = -0.0002x + 0.2125$; $r^2 = 0.006$, $P < 0.001$). ΔT in *E. grandiflora* had a more linear increase during the dry season ($y = 0.001x - 0.0636$; $r^2 = 0.254$, $P < 0.001$) compared to *C. tessellata* at greater PPFD_{site} and, overall, ΔT varied less in *E. grandiflora* at higher PPFD_{site} during the dry season.

3.5. Structural equation model (SEM)

The best SEM model that explained changes in T_{leaf} is depicted in Fig. 6. This model was run using all daytime 10-min measurements for the wet and the dry season, and for each species individually. Other models that included alternative paths and other variables such as RH and VPD were rejected ($\chi^2 > 200$, $P < 0.001$). Although we transformed all variables to their natural logarithm to improve normality and linearity of the data, we will refer to the variables as the non-transformed form. Time of day (TOD) had a strong relationship with PPFD_{site} in both seasons ($P < 0.001$), especially during the dry season (path coefficient $\beta = 0.62$ for *C. tessellata* and $\beta = 0.6$ for *E. grandiflora*). However, although significant, the relationship between TOD and T_{air} was weaker in both species during the wet season ($\beta = 0.09$). T_{air} and PPFD_{site} were more predictable by TOD during the dry season.

PPFD_{site} was a good predictor of T_{air} in both seasons and in both species ($\beta > 0.62$), and it also had a strong relationship with PPFD_l, especially in *E. grandiflora* ($\beta = 0.93$ and 0.91 for the wet and dry season respectively; Fig. 6). PPFD_{site} had a significant effect in T_{leaf} during the wet season (especially in *C. tessellata*; $\beta = 0.39$) but not during the dry season ($\beta = 0.01$ and 0.04 for *C. tessellata* and *E. grandiflora* respectively). However, PPFD_l had a significant effect on T_{leaf} during the dry season ($\beta = 0.11$ and 0.15 for *C. tessellata* and *E. grandiflora* respectively). T_{air} was the main predictor of T_{leaf} for both species, especially during the dry season ($\beta > 0.9$; Fig. 6). During the wet season this effect was stronger in *E. grandiflora* ($\beta = 0.77$ vs. 0.53 in *C. tessellata*). Overall, the SEM models explained more than 90% of T_{leaf}

variance in both seasons and both species (Fig. 6).

4. Discussion

This is the first study, to our knowledge, that compares microclimatic conditions of a páramo during both wet and dry seasons. It is also the first attempt at determining the quantitative and correlative relationships between T_{air} , T_{leaf} , under natural sunlight (PPFD) regimes characteristic of a páramo. Models often evaluate the effects of increasing air temperature on ecosystem processes (Cramer et al., 1999; Rowland et al., 2015). However, as mentioned in Rey-Sánchez et al. (2016), using T_{air} to accurately simulate T_{leaf} in the field can generate large errors. T_{air} is not the only climate variable that drives T_{leaf} . Incident sunlight also plays an important quantitative role in generating field values of T_{leaf} both above and below T_{air} (Rey-Sánchez et al., 2016). In addition, incorporating the diverse physiological responses of plants to air temperature in models is important to accurately predicting carbon and water balance under future scenarios of climate change.

In summary of the results presented here, T_{leaf} was strongly correlated with T_{air} , although there were important deviations. Differences between T_{leaf} and T_{air} were on average 0.2 and 0.3 °C for the wet and dry season, respectively. However, maximum daytime ΔT was as high as 14 °C in *C. tessellata* and 10 °C in *E. grandiflora* during the dry season compared to ca. 12 °C during the wet season for both species. At night, greater cloud cover during the wet season generated a closer coupling between T_{leaf} and T_{air} , and T_{leaf} was never below 0 °C (Fig. 4).

4.1. Leaf and air temperatures

The results presented here are consistent with those reported in Sanchez et al. (2014) and for other species of *Espeletia* found in Venezuela where ΔT approached 15 °C for the inner leaves of rosettes (Meinzer et al., 1994; Rada, 2016). Another study that compared leaf

temperature to environmental drivers in a semi-deciduous tropical forest of Panama (Rey-Sánchez et al., 2016), found that leaves tend to be warmer than T_{air} during the wet season, possibly due to lower wind speeds and, thus, lower convective heat exchange. However, wind speeds measured at our study site were not lower in the wet versus dry season (see Methods). An alternative explanation may be differences in seasonal and diurnal leaf orientations (Fig. 1; Sanchez et al., 2014). Because high levels of incident solar radiation can warm leaves (as well as T_{air}), we believe that species such as *C. tessellata* may be able to adjust leaf orientation depending on incident radiation. Leaf orientation was observed to be more horizontal during the daytime of the wet season than during the daytime of the dry season, when they are almost completely vertical (Sanchez, unpublished data). In addition, *E. grandiflora*, leaves are more pubescent and tend to be less perpendicular to the incident solar beam than in *C. tessellata* (Sanchez et al., 2014). Although pubescence can potentially be an important mechanism to reduce incident sunlight (e.g. Ehleringer, 1984; discussed in Meinzer et al., 1994), leaves of both species remained warmer than T_{air} for most of the day during both wet and dry seasons. Few studies to date have studied plant or leaf functional traits in the ecosystem of páramo (e.g., Castrillo and Simoes, 1997; Almeida et al., 2012); therefore, additional research on the interplay of these traits and plant responses to T_{air} are needed to better understand their adaptations to the current abiotic conditions.

In the Panamanian forest, air temperatures were high but plants were reported to use transpirational cooling to reduce T_{leaf} , possibly as a mechanism to keep leaves closer to the optimal temperature for photosynthesis (Helliker and Richter, 2008). This may also be the case of species such as *E. grandiflora* (Meinzer et al., 1994; Rada et al., 2012; Sanchez et al. unpubl. data). Additionally, in the páramo, temperatures were often below 0 °C during the night, which can cause plant frost (Rada, 2016). During the dry season especially, sky-exposed microsites and the accumulation of cold air next to the ground generated T_{leaf} values well below T_{air} (Jordan and Smith, 1995; Germino and Smith, 1999). In the wet season we did not registered T_{leaf} below 0 °C (Fig. 3) and this may be partly explained by a more common cloud cover during these months. Clouds restrict the emissions of thermal radiation to space (Ramanathan et al., 1989), maintaining T_{leaf} and T_{air} above freezing and T_{leaf} more coupled to T_{air} .

The most recent global climate models not only suggest that there will be increases in temperature of up to 5–6 °C warmer than present air temperatures (IPCC WG2 TSU, 2014) and changes in precipitation but also changes in cloud patterns (IPCC 2014). Given that air temperature in most instances is closely coupled to leaf temperature and thus, to respiration and photosynthesis (Berry and Björkman, 1980), increasing temperatures may result in lower net carbon gain in the páramo species studied. On the other hand, clouds affect incoming solar radiation and precipitation; given that clouds are already changing their distributions (Norris et al., 2016), this could result in more radiation absorbed, a more pronounced greenhouse effect, and possibly, more extreme $PPFD$ events. Although more information on the eco-physiology of páramo species is needed, the specific results reported here indicate future impacts due to the warmer air temperatures and potential shifts in the length and occurrence of the wet/dry seasons of the under current climate change scenarios.

4.2. Cloud effects and precipitation

Based on our results, $PPFD_{site}$ had an important relationship with both, T_{air} and T_{leaf} (Figs. 5 and 6; A1, A2). Above $\sim 400 \mu\text{mol m}^{-2} \text{s}^{-1}$ there is a significant linear relationship between $PPFD_{site}$ and T_{leaf} for both seasons and both species (Fig. A2). The $PPFD_{site}$ events (as a proxy to GSR), higher than the Solar Constant and higher than $3000 \mu\text{mol m}^{-2} \text{s}^{-1}$ may have an important warming effect on T_{leaf} , especially during the wet season because T_{air} is cooler overall (Figs. 2 and 5).

The high weather variability of the páramo (similar to other tropical alpine areas) can result in rain, ice, sleet, or fog on almost any day of the year that may abruptly alternate with clear skies and elevated leaf and air temperatures (Luteyn, 1999). These changes are often due to rapidly changing cloud types and patterns on the order of minutes. A previous study by Sanchez et al. (2014) showed that during a few days in March of 2012 (wet season), light could vary abruptly within a few minutes. These authors also measured values of incident $PPFD$ above $3000 \mu\text{mol m}^{-2} \text{s}^{-1}$, well over the Solar Constant (Pearcy et al., 1989). In the present study, we recorded continuous values of $PPFD_{site}$ for a period of 14 months (Fig. A4) and frequently found values well above $3000 \mu\text{mol m}^{-2} \text{s}^{-1}$ (up to $\sim 3650 \mu\text{mol m}^{-2} \text{s}^{-1}$). Other studies have found similarly high values that were associated with specific cloud patterns (Gu et al., 2001; Dye et al., 2009), although the most common levels of insolation are below ca. $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ (as found in our study) due to complete cloud cover (Diemer, 1996; Figs. 2, A4). Körner (2003) suggests that these extremes can occur when a thin layer of strato-cirrus clouds contributes to $PPFD$ via diffuse light transmitted by the clouds, in addition to the direct solar radiation, increases total incident solar radiation. In addition, these unusually high $PPFD$ can occur when larger nimbostratus clouds have gaps with direct sunlight passing through and possibly amplified by multiple reflections from the sides of the cloud channel (Smith et al. unpublished data). In our study site, it was not uncommon to see cirrus clouds alternating with full cloud immersion (fog) at any moment of the day (but especially in the early morning and evening), and clear skies alternating with large cumulus (storm-like) clouds during the daytime (Sanchez pers. obs.) and coinciding with these high sunlight episodes (Figs. A3 and A4).

In addition, plants in these ecosystems have to withstand short-term but extreme $PPFD$ values that are unlikely to occur at lower altitudes (Smith and Geller, 1980; Körner, 2003), and these extremes not only affect photosynthetic induction (Martins et al., 2013) but may also have photoinhibitory effects on photosynthesis (e.g., Germino and Smith, 2000; Maher and Germino, 2006).

With few exceptions, most páramos in Colombia are influenced by a low pressure trough because of their proximity to the Equator (Luteyn, 1999). Thus, they are in general humid (70–85% RH) during most part of the year due to rain, clouds and fog (Sarmiento, 1986; Luteyn, 1999). Many páramos, such as the case of Chingaza, receive more than an average 2000 mm or precipitation per year (Tol and Cleef, 1994; Cardenas et al., 2002). Given that our field site of Laguna Seca is found in an area with unimodal precipitation regime and a short three-month dry season (December to February), it is not surprising that average RH for 2013 in Chingaza was 95% explaining the low annual VPD values (average of 0.07 kPa). Plants in this area tend to have abundant water available through most of the year (March to December), although water stress is not uncommon in January and February (Sanchez, unpublished data).

4.3. Structural equation model (SEM)

According to our empirical model (SEM) more than 90% of the variation in T_{leaf} was explained as a function of T_{air} and $PPFD$ measured at both the site and leaf level (Fig. 6). In *C. tessellata*, the SEM model explained more of the variation that occurred during the dry season (94%) while *E. grandiflora* showed no differences between seasons. In the dry season, the main driver of T_{leaf} was T_{air} , with small contributions of $PPFD$ (Fig. 6). In the wet season T_{air} was the main contributor of T_{leaf} but there was also a significant contribution by $PPFD$ (especially in *C. tessellata*). Interestingly, $PPFD_{site}$ had an important effect in determining T_{air} , an effect even more pronounced than time of day. Thus, radiation heating has both a direct and an indirect (via T_{air}) effect on T_{leaf} . The warming effect of incident sunlight on T_{leaf} is relatively well known compared to the direct influence of sunlight on heating the air (T_{air}) adjacent to individual plants. Thus, T_{air} measured at central locations at research sites may not reflect effects of T_{air} on T_{leaf} . Yet, this effect of

microsite on T_{air} has been described in some detail as far back as Geiger's (1950) definition of "pseudo-conduction", whereby air is heated by nearby sun-exposed objects that radiate longwave radiation back to the air (both water vapor and CO_2 are strong longwave absorbers and emitters), thus increasing air temperature via a mini-greenhouse effect. In addition, the proximity of plants to the ground surface enhances water vapor and CO_2 concentrations of the air, especially under still wind conditions. It is worth noting that at higher elevations, this heating of the air will be less due to the lower air temperatures and, thus, lower water vapor content of the air (Geiger et al., 2009). The effect of elevation on air CO_2 content next to the soil surface is less known. Regardless, microclimate measurements of T_{air} appear to be necessary for accurate energy balance calculations of T_{leaf} versus only site measurements of T_{air} at standard 2 m heights.

The SEM constructed within this study was similar to the one obtained for a lowland semi-deciduous tropical forest in Panama, where T_{air} was also the main driver of T_{leaf} and $PPFD$ incident on the leaf was the second most important driver (Rey-Sánchez et al., 2016). However, in the Panama forest $PPFD$ had a much stronger effect on T_{leaf} variation in the wet season compared to the wet season of the present study. In addition it was $PPFD_{site}$ and not $PPFD_l$ that had a more important effect on T_{leaf} , indicating that the general warming of the air through $PPFD$ could have been affecting T_{leaf} . Such an idea is consistent with the proximity of the páramo plants to the ground, which makes them more dependent on the radiation absorbed by the soil. Therefore, there seems to be a consistent pattern in which both T_{air} and $PPFD$ influence T_{leaf} , but their relative effect depends on season.

5. Conclusions

Data describing the influence of cloud dynamics on air and leaf temperatures are rare, especially in high elevation tropical alpine zones (Körner, 2002; Pellicciotti et al., 2011; Sanchez et al., 2014). Based on our results here for two common species of the páramo, using T_{air} as a substitute of T_{leaf} in climate models that predict carbon/water balance can deviate, on average, only between 0.2–0.5 °C, but can vary by up to 14 °C at any given moment. Although T_{air} was the best predictor of T_{leaf} , contributions of $PPFD$ values cannot be neglected, especially during the wet season (Figs. 5 and 6). Because sunlight incidence is highly variable in Chingaza, as well as other alpine ecosystems, due to dynamic cloud regimes (Scherrer and Körner, 2010; Fernandez Monteiro et al., 2011; Sanchez et al., 2014), large differences in air and leaf temperature occur, and utilizing air temperature as a proxy for leaf temperature will generate large errors in predicting the impacts of global warming on páramo vegetation.

One of the main predictions of future climate change is that warming air temperatures will result in the advance of the subalpine forest into the alpine, reducing the spatial extent of the alpine zone, and potentially include concomitant losses of alpine biodiversity and ecosystem services (Díaz et al., 2007; Buytaert et al., 2011). An increase in air temperature and solar radiation could also increase the temperature of páramo topsoil, contributing further to an upward movement of the upper forest timberline from its current position (Buytaert et al., 2011). Although some recent studies have demonstrated that the advance of alpine treelines will require more than just an increase in global temperature (e.g. precipitation) and that any response will most likely be species-specific (e.g., Barbeito et al., 2012; Rehm and Feeley, 2015a). For example, temperature and shading are two of the most important abiotic variables that determine tree seedling survivorship in high mountains (Germino and Smith, 1999, 2002; Bader et al. 2007; Rehm and Feeley, 2015b). Although sunlight can be a limiting factor for carbon assimilation, too much incident sunlight in tropical and temperate alpine sites can also be detrimental (Germino and Smith, 2000; Sanchez et al., 2014; Sanchez and Smith, 2015; Sanchez et al., 2016). Additional research on the ecophysiological response to altered sunlight regimes is needed to evaluated future climate change effects on the

distribution of the páramo.

Conflict of interest

None.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agrformet.2018.01.033>.

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